The influence of daily thermoperiods on the duration of seasonal cycle of development in the ants *Myrmica rubra* L. and *M. ruginodis* Nyl.

E. B. Lopatina and V. E. Kipyatkov

Laboratory of Entomology, Biological Research Institute of St. Petersburg University, 2 Oranienbaumskoye shosse, Petergof, St. Petersburg, 198904, Russia
e-mail: el@socium.usr.pu.ru

Department of Entomology, Faculty of Biology, St. Petersburg University, 7/9 Universitetskaya emb., St. Petersburg, 199034, Russia

Abstract – Experiments were made comparing the pattern of colony development cycles under different thermoperiods. Populations of *Myrmica ruginodis* and *M. rubra* from two regions were compared: near Vyritsa (St. Petersburg region) and near Borisovka (Belgorod region). Three experiments were made. In the first, we used ants collected from the field before the appearance of the first eggs and in the other two we used the ant colonies that had been given a laboratory hibernation at 3–5°C for 3–4 months. Experimental cultures each consisting of 150 workers and one queen were maintained in photo thermostatic chambers under 12-hours thermoperiods (15/25°C and 10/25°C) or at constant temperatures (20 and 17.5°C equivalent to mean daily temperatures of the thermoperiods) in a combination with long (20 h) or short (12 h) days. The eggs laid by queens were allowed to develop into rapid brood pupae and diapausing larvae (slow brood). Thermoperiods were found to stimulate longer oviposition and pupation in cultures of both species at long-day conditions, which resulted in greater production of rapid brood pupae due to the postponement of the onset of larval diapause. The effects of thermoperiods under short-day conditions was quite different between the two species studied. Under short days, thermoperiods extended the seasonal cycle delaying the diapause induction *M. ruginodis* from Belgorod population in the same way as under long days. Whereas in *M. rubra* from St. Petersburg region under short days, the effect of fluctuating temperature appeared to be the reverse of long days: thermoperiods caused earlier onset of diapause in both queens and larvae.

However, it remains uncertain whether this effect of thermoperiods, facilitating the onset of diapause under short days, is a specific attribute of *M. rubra* or a general characteristic of *St. Petersburg* *Myrmica* populations.

Keywords: Formicidae, *Myrmica*, seasonal cycle, oviposition, rapid brood, pupation, diapause, temperature, thermoperiod, photoperiod, control.

Introduction

It is well known for a many organisms that fluctuating, unstable temperature, especially regular daily temperature rhythms, are more natural, more adequate and favourable for development and reproduction than the constant temperature regimes which are generally employed in laboratory experiments (Odum, 1971; Ratte, 1985). The development of insects often proceeds at quite different rates at fluctuating and equivalent constant temperatures (Ludwig and
Cable, 1934; Ratte, 1985). It has also been shown that daily temperature rhythms (thermoperiods) exert significant effects on insect development, size and weight, longevity, fecundity (Ratte, 1985), diapause induction and termination (Beck, 1983; Danks, 1987) and behaviour (e.g. circadian rhythms — see Beck, 1983).

Data on the influence of thermoperiods on the development and behaviour of ants are scarce. It is well known, however, that distinct daily rhythms of temperature are usually inherent to microclimate of ant nests, especially in species of temperate climates (Brian, 1983). Thus, daily fluctuations of temperature should be considered as natural for most ants and their influence on ant development and behaviour deserves special attention. Buschinger (1973) demonstrated that daily rhythms of temperature were significantly more favourable for the development of brood in ants of the tribe Formicoxenini, especially during the second part of summer i.e. in the period of diapause induction and diapause growth of larvae. He succeeded in making a special program to imitate different seasons of a year, consisting of three different thermoperiods, which he used for laboratory breeding of various formicoxenine ants and allowed the compression of the whole annual cycle of colony development into 3.5–4 months. Elmes and Wardlaw (1983) reported experiments showing that the developmental times of large hibernated larvae of *Myrmica rubra* reared by workers at 12-hours thermoperiods with temperature range 15–25°C and at equivalent constant temperature of 20°C were not significantly different, whereas thermoperiods 6 h at 25°C/18 h at 15°C caused a little slower development compared to that obtained at equivalent constant temperature.

Our preliminary experiments (Lopatina and Kipyatkov, 1990a,b) carried out with the use of several ant species (*Camponotus xerxes*, *Formica cinerea*, *Lepisiota semenovi*, *Myrmica rubra*, *Monomorium kusnezovi*, *M. ruzskyi*, *Plagiolepis compressus*, *Tapinoma karavaievi*, *Tetramorium caespitum*) revealed three basic effects of thermoperiods on ant development: (1) acceleration of egg and larval development; (2) increase of queen fecundity, colony productivity, brood survival and successfulness of development; (3) extension of seasonal cycle of non-diapause development owing to postponed onset of diapause. Later, working on *Camponotus herculeanus* and *C. xerxes*, Lopatina and Kipyatkov (1993) found that 12-hours thermoperiods 14/32, 16/30 and 20/30°C accelerated egg and larval development by 14–20%, significantly increased queen productivity and brood survival and promoted more prolonged non-diapause development in comparison with constant temperatures that were equivalent to the mean daily temperature of the respective thermoperiod. Daily thermoperiods 15/25, 16/30 and 20/30°C were shown to be the most favourable temperature regimes for *Formica cinerea*, *F. clara*, *F. fusca*, *F. japonica* and *F. lemani* unless their daytime (i.e. the higher) temperature exceeded the upper limit of a species’ optimal zone. Thermoperiods also accelerated significantly the rate of brood development and prolonged the queen oviposition period in *F. cinerea*, *F. fusca* and *F. lemani* (Kipyatkov and Lopatina, 1993).

For us, the most interesting aspect of thermoperiodism in ants is its role in the control of seasonal development and onset of diapause (Kipyatkov, 1993), therefore we have studied this using two of the most common European *Myrmica* species – *M. rubra* and *M. ruginodis*. The annual brood production of a *Myrmica* colony is split into two parts – rapid or summer brood (i.e. larvae developing from eggs without a diapause and pupating during the same warm season) and slow or winter brood, i.e. larvae that fall in diapause in late summer, continue to grow slowly in autumn, hibernate and pupate during the next warm season (Brian, 1951, 1957; Cammaerts, 1977; Elmes, 1991). The seasonal cycle of development of *Myrmica* species is known to be controlled by an endogenous timer along with external ecological factors – temperature and photoperiod. These factors adjust the date of diapause arising to the climatic characteristics of a given year. In late summer the lower temperature and short days induce the diapause thus curtailing the period of development (Kipyatkov, 1974, 1977, 1979, 1990, 1993, 1995). Hence, the main parameters of *Myrmica* seasonal cycle are the duration of queens’ oviposition and the length of the period of rapid brood puation, both of which depend on the time of onset of diapause in larvae and queens in late summer (Kipyatkov, 1993).
Materials and methods

Stock colonies of *M. rubra* and *M. ruginodis* were collected in two regions: near Borisovka (Belgorod region) and near Vyrtsa (St. Petersburg region). At Borisovka both species live under the canopy of oak deciduous forest nesting mainly in rotting dead wood. The Vyrtsa site was in coniferous pine woodland were ants build nests mostly in moss hillocks and very rarely in dead wood. Both sites were at low altitudes.

In the first experiment (1) we used ants collected in spring before the appearance of the first eggs: colonies of *M. ruginodis* from Borisovka collected in early April and colonies of *M. rubra* from Vyrtsa collected at the end of May. Experimental cultures were established in few days after the collection and placed immediately into experimental regimes. For two other experiments (2 and 3) we used ant colonies from the same two sites but after a hibernation in laboratory at 3–5°C for 3–4 months. Thus, they were physiologically in early spring state, just at the beginning of annual cycle of development (Brian, 1955; Kipyatkov, 1993). Following the artificial hibernation ants were kept at 10°C and at 15°C (for a week at each temperature) and after that were placed directly to the experimental regimes.

Experimental groups usually consisted of 150 workers and one queen. In experiment 2, 30 medium and large overwintered larvae were also added to each group. Ant groups were maintained in plastic laboratory nests with approximately 100% humidity and ample food (cockroaches *Nauphoeta cinerea* cut into pieces and 15% sucrose solution) in photothermostatic chambers. We used two 12-hours thermoperiods (15/25°C and 10/25°C) and two constant temperatures (20 and 17.5°C) that were equivalent to mean daily temperatures of the respective thermoperiods. Two photoperiods were used in combination with the temperature regimes—long (20 h) days and short (12 h) days. In all experiments the ants were kept under the same regimes throughout.

Queens laid eggs right from the start of experiment 1 because they came from natural colonies and were already active and ready for oviposition. In experiments 2 and 3 queens needed some period following hibernation for full ovarian development, and thus oviposition began a little later. Workers were allowed to rear the eggs into the rapid brood pupae and diapausing larvae. Cultures were examined once per week or sometimes per two weeks, and all pupae produced during the preceding period were removed and counted (they were not returned to nests) and the presence of eggs and early instars larvae were checked. In experiment 1 when pupation stopped and the eggs and early instar larvae had disappeared, all the remaining third instar diapausing larvae were counted. During all manipulations the ants were anaesthetised by a short (up to 30 seconds) exposure to carbon-dioxide which is known to have no negative effect on brood rearing (Wardlaw, 1995).

From these data we calculated the following parameters for each group: the interval between the beginning of oviposition and the disappearance of eggs (i.e. the period of eggs presence), the duration of rapid brood pupation (i.e. the period from the beginning until the end of pupation) and the number of rapid brood pupae produced. In experiment 1 we also obtained the number of diapausing larvae reared, the total number of brood produced (i.e. rapid brood plus diapausing larvae) and the share (per cent) of the rapid brood in the total brood.

Results

Experiment 1

Distinct photoperiodic effects were observed for both species: the duration of pupal production and the quantity of rapid brood pupae reared were on the average significantly greater under 20 h than under 12 h both at thermoperiods and constant temperature (Fig. 1a; Tab. 1, 2). The mean period until eggs disappeared at constant 20°C in *M. rubra*, appeared to be independent of photoperiod but in *M. ruginodis* it was notably shorter at 12 h. Unfortunately, all cultures at 15/25°C 20 h were killed by a sudden temperature rise due to equipment failure on 7 August, and only the data on the number of pupae reared until that date were obtained.
Table 1. Duration of seasonal cycle and number of rapid brood produced in cultures of Myrmica rubra from St. Petersburg population under thermoperiods or constant temperature at long or short days.

<table>
<thead>
<tr>
<th>Experimental regimes and parameters</th>
<th>Period until eggs disappear -ance (days)</th>
<th>Rapid brood pupation</th>
<th>Number of larvae in diapause (%)</th>
<th>Total number of brood produced</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>duratio n (days)</td>
<td>number</td>
<td>share</td>
</tr>
<tr>
<td>20°C 20 h</td>
<td>min</td>
<td>84</td>
<td>28</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>max</td>
<td>105</td>
<td>42</td>
<td>48</td>
</tr>
<tr>
<td></td>
<td>n = 4</td>
<td>mean</td>
<td>98</td>
<td>38</td>
</tr>
<tr>
<td></td>
<td>S.D.</td>
<td></td>
<td>6.8</td>
<td>15.5</td>
</tr>
<tr>
<td>15/25°C 20 h</td>
<td>min</td>
<td>51</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>max</td>
<td>95</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>n = 4</td>
<td>mean</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>S.D.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20°C 12 h</td>
<td>min</td>
<td>95</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>max</td>
<td>109</td>
<td>14</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>n = 2</td>
<td>mean</td>
<td>A 102</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>S.D.</td>
<td></td>
<td>9.9</td>
<td>4.6</td>
</tr>
<tr>
<td>15/25°C 12 h</td>
<td>min</td>
<td>52</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>max</td>
<td>95</td>
<td>22</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>n = 4</td>
<td>mean</td>
<td>A 68</td>
<td>9</td>
</tr>
<tr>
<td></td>
<td>S.D.</td>
<td></td>
<td>18.6</td>
<td>11.0</td>
</tr>
</tbody>
</table>

The identical letters in the same column denote the means that differ significantly (P<0.05) from each other (the comparison was done only between thermoperiods and constant temperatures under long and short day regimes separately).

* All groups at this regime were killed by a sudden temperature rise due to equipment failure on the 10th week of the experiment and only the data on the number of pupae reared until that date are available.

*M. rubra* cultures had much shorter cycle of development in comparison to *M. ruginodis* due to a great latitudinal difference between sites of collection of the stock colonies of *M. rubra* (St. Petersburg) and *M. ruginodis* (Belgorod) (see Kipyatkov and Lopatina, 1997 – pp. 195-206 in this volume). Under 12 h conditions only a few rapid brood pupae were reared by *M. rubra* groups and the differences between thermoperiod and constant temperature appeared to be insignificant (Fig. 1a; Tab. 1). However, under 20 h the cultures at 15/25°C had produced significantly more pupae by the time of their premature death in comparison with ants at constant 20°C (Fig. 1a; Tab. 1) and we might suppose that they would have reared even more pupae if they had lived. Another interesting difference was the significantly longer period of presence of eggs at 20°C SD compared to 15/25°C SD (Tab. 1), which means that queen diapause began sooner at thermoperiods than at constant temperature.

Owing to the longer cycle of development in cultures of *M. ruginodis* from Belgorod region they produced significantly more pupae under 12 h than *M. rubra* groups. The differences between constant and fluctuating temperatures were quite apparent in these conditions: thermoperiod 15/25°C caused significantly longer oviposition and pupation and much greater rapid and slow brood production in comparison to constant 20°C (Fig. 1b; Tab. 2). Thus unlike *M. rubra*, 12 h thermoperiods caused longer oviposition by *M. ruginodis* queens in comparison with constant 20°C. Under 20 h the cultures at 15/25°C reared fewer pupae before their death in
The influence of daily thermoperiods on the development of *Myrmica* ants

comparison to cultures at 20°C (Tab. 2). But they could proceed to rear larvae (which is clear from Fig. 1b) and would produce even more pupae than cultures at constant temperature.

**Table 2.** *Duration of seasonal cycle and number of rapid brood produced in cultures* *Myrmica ruginodis* *from Belgorod population under thermoperiods or constant temperature at long or short days.*

<table>
<thead>
<tr>
<th>Experimental regimes and parameters</th>
<th>Period until eggs disappearance (days)</th>
<th>Rapid brood pupation</th>
<th>Number of larvae in diapause (%)</th>
<th>Total number of brood produced</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>duration (days)</td>
<td>number</td>
<td>S.D.</td>
</tr>
<tr>
<td>20°C 20 h min</td>
<td>104</td>
<td>41</td>
<td>59</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>max</td>
<td>104</td>
<td>59</td>
<td>134</td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>104</td>
<td>49</td>
<td>94</td>
</tr>
<tr>
<td></td>
<td>n = 3</td>
<td>S.D.</td>
<td>9.2</td>
<td>37.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15/25°C 20 h min</td>
<td>104</td>
<td>49</td>
<td>49</td>
<td>111</td>
</tr>
<tr>
<td></td>
<td>max</td>
<td>104</td>
<td>149</td>
<td>111</td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>104</td>
<td>93</td>
<td>180</td>
</tr>
<tr>
<td></td>
<td>n = 2</td>
<td>S.D.</td>
<td>7.5</td>
<td>13.1</td>
</tr>
<tr>
<td>20°C 12 h min</td>
<td>104</td>
<td>41</td>
<td>59</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>max</td>
<td>104</td>
<td>59</td>
<td>134</td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>104</td>
<td>49</td>
<td>94</td>
</tr>
<tr>
<td></td>
<td>n = 3</td>
<td>S.D.</td>
<td>9.2</td>
<td>37.7</td>
</tr>
<tr>
<td>15/25°C 12 h min</td>
<td>104</td>
<td>49</td>
<td>28</td>
<td>93</td>
</tr>
<tr>
<td></td>
<td>max</td>
<td>104</td>
<td>149</td>
<td>111</td>
</tr>
<tr>
<td></td>
<td>mean</td>
<td>104</td>
<td>93</td>
<td>180</td>
</tr>
<tr>
<td></td>
<td>n = 3</td>
<td>S.D.</td>
<td>7.5</td>
<td>13.1</td>
</tr>
</tbody>
</table>

The identical letters in the same column denote the means that differ significantly (P < 0.05) from each other (the comparison was done only between thermoperiods and constant temperatures under long and short day regimes separately).

* All groups at this regime were killed by a sudden temperature rise due to equipment failure on the 17th week of the experiment and only the data on the number of pupae reared until that date are, therefore, available.

**Experiment 2**

In this experiment, which was carried out after an artificial hibernation, only 20 h conditions were used because only a few stock colonies of *M. rubra* from St. Petersburg and *M. ruginodis* from Belgorod, were available. We did not count the number of rapid brood pupae produced and only observed the duration of oviposition and pupation in ant cultures. The results appeared to be quite similar to those obtained in experiment 1: the mean periods of egg presence and pupation were significantly longer under thermoperiods 15/25°C as compared to constant 20°C (Tab. 3).

**Experiment 3**

This experiment was also carried out after an artificial hibernation. We used thermoperiod 10/25°C which was a larger amplitude (15°C instead of 10°C) between high and low temperatures than used in the two previous experiments. Hence we used a lower mean equivalent temperature (17.5°C instead of 20°C).

No effects of day-length were found at constant 17.5°C in cultures of *M. rubra* originating from St. Petersburg (Tab. 4). These results accord well with our previous findings (Kipyatkov,
that the photoperiodic responses in *Myrmica* observed at higher temperatures, are not always apparent at 17°C. Thus it was all the more interesting that the influence of photoperiod was evident under fluctuating temperature conditions: the cultures at 10/25°C 20 h on the average had significantly longer periods of egg presence and pupation, and produced many more pupae than the cultures at 10/25°C 12 h (Tab. 4).

**Figure 1.** Rapid brood pupation per culture per week in *Myrmica rubra* (St. Petersburg population) and *M. ruginodis* (Belgorod population) under thermoperiods or constant temperature at long or short days.

In *M. rubra* cultures from Belgorod site the mean periods of egg presence and pupation, were longer at 10/25°C 20 h and the cultures reared on the average more rapid brood pupae in comparison with cultures at constant 17.5°C 20 h (Tab. 4). At St. Petersburg site, the effects of thermoperiods on the development of *M. rubra*, the difference between 20 h and 12 h appeared to be the opposite. Under 20 h conditions thermoperiods clearly stimulated longer oviposition and pupation and greater rapid brood production as compared to constant temperature, similarly to the effects observed in *M. rubra* from Belgorod site. However, under 12 h the oviposition and pupation cycles were on the average shorter and the mean number of pupae reared was much less at 10/25°C than at constant 17.5°C (Tab. 4). This indicated that thermoperiods caused earlier
onset of diapause thus reinforcing the short-day effects, as was observed in experiment 1 for oviposition in the same species.

In contrast to M. rubra the effects of thermoperiods on the development of M. ruginodis cultures from Belgorod population were always positive, i.e. stimulating longer oviposition and pupation and greater rapid brood production both at 20 h and 12 h (Tab. 5). These results are in good accordance with the data obtained for Belgorod population of M. ruginodis in experiments 1 and 2 (Tab. 2, 3). It should also be noted that the photoperiodic responses in the cultures of M. ruginodis, like to those of M. rubra, were quite apparent under the fluctuating temperature regime but absent under the constant 17.5°C (Tab. 4).

Table 3. Duration of oviposition and pupation cycles in Myrmica rubra and M. ruginodis cultures under thermoperiods or constant temperature at long (20 h) days (after artificial hibernation).

<table>
<thead>
<tr>
<th>Species and population</th>
<th>Experimental regimes and parameters</th>
<th>The period until:</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>eggs disappearance</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(days)</td>
</tr>
<tr>
<td>M. rubra</td>
<td>20°C min</td>
<td>81</td>
</tr>
<tr>
<td></td>
<td>max</td>
<td>95</td>
</tr>
<tr>
<td></td>
<td>mean S.D.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A 90 S.D.</td>
<td>8.1</td>
</tr>
<tr>
<td></td>
<td>15/25°C min</td>
<td>103</td>
</tr>
<tr>
<td></td>
<td>max</td>
<td>149</td>
</tr>
<tr>
<td></td>
<td>mean S.D.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A 133 S.D.</td>
<td>26.6</td>
</tr>
<tr>
<td>M. ruginodis</td>
<td>20°C min</td>
<td>124</td>
</tr>
<tr>
<td></td>
<td>max</td>
<td>131</td>
</tr>
<tr>
<td></td>
<td>mean S.D.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A 129 S.D.</td>
<td>3.1</td>
</tr>
<tr>
<td></td>
<td>15/25°C min</td>
<td>110</td>
</tr>
<tr>
<td></td>
<td>max</td>
<td>189</td>
</tr>
<tr>
<td></td>
<td>mean S.D.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>A 152 S.D.</td>
<td>37.5</td>
</tr>
</tbody>
</table>

The identical letters in the same column denote the means that differ significantly (P<0.95) from each other (the comparison was done within each species separately).

**Discussion**

Besides demonstrating yet again that photoperiod has a role as an external factor controlling the seasonal cycle of development in Myrmica colonies, our results also indicate the existence of an interesting effect of low temperature inhibition of photoperiodic responses which is a consequence of the rule of thermal optimum of photoperiodic responses well-known in other insects (Danilevski, 1965; Beck, 1980; Danks, 1987) and also in Myrmica (Kipyatkov, 1977; Kipyatkov and Lopatina, 1997). Thus, photoperiodic control of oviposition and larval development in Myrmica colonies is most pronounced and important in optimal thermal conditions.

The most interesting result from our experiments described in this paper, concerns the effects of fluctuating temperature on the duration of the seasonal cycle of oviposition and development
in ant colonies. The daily 12-hours thermoperiods 10/25 and 15/25°C were found to stimulate longer oviposition and pupation in colonies of both species studied at long-day conditions which resulted in greater production of rapid brood pupae owing to postponed onset of diapause in larvae developing from eggs. This effect of thermoperiod is in good accordance with our earlier findings for other ant species (Lopatina and Kipyatkov, 1990a,b). However, the effects of thermoperiods on the oviposition and development under short-day conditions seemed to be quite different in the two species tested.

Table 4. Duration of seasonal cycle and number of rapid brood produced in cultures of Myrmica rubra under thermoperiods or constant temperature at long or short days (after artificial hibernation).

<table>
<thead>
<tr>
<th>Place</th>
<th>Experimental regimes and parameters</th>
<th>Periods (in days) of:</th>
<th>Rapid brood pupae number</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>eggs presence</td>
<td>rapid brood pupation</td>
</tr>
<tr>
<td>Belgorod</td>
<td>17.5°C min 20 h max n = 4</td>
<td>99</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>132</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>mean 123</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>S.D. 15.9</td>
</tr>
<tr>
<td></td>
<td>10/25°C min 20 h max n = 3</td>
<td>97</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>mean 130</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>S.D. 29.2</td>
</tr>
<tr>
<td>St. Petersburg</td>
<td>17.5°C min 20 h max n = 4</td>
<td>86</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>mean 99</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>S.D. 11.1</td>
</tr>
<tr>
<td></td>
<td>10/25°C min 20 h max n = 4</td>
<td>121</td>
<td>34</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>mean 135</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>S.D. 14.2</td>
</tr>
<tr>
<td></td>
<td>17.5°C min 12 h max n = 3</td>
<td>89</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>mean 108</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>S.D. 16.7</td>
</tr>
<tr>
<td></td>
<td>10/25°C min 12 h max n = 4</td>
<td>84</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>mean 94</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>S.D. 9.5</td>
</tr>
</tbody>
</table>

The identical letters in the same column denote the means that differ significantly (P<0.95) from each other (the comparison was done only between thermoperiods and constant temperatures under long and short day regimes and within each population separately).

In M. ruginodis from Belgorod, thermoperiods extended the seasonal cycle delaying the onset of diapause under short days as well as under long days. Whereas in M. rubra from St. Petersburg region, the effect of fluctuating temperature under short days appeared to be reverse: thermoperiods caused earlier diapause onset in both experiments (in experiment 1 for queen diapause, in experiment 3 both for queen and larval diapause). The situation looks like if thermoperiods
The influence of daily thermoperiods on the development of *Myrmica* ants really reinforce the effects of photoperiods prolonging non-diapause development at long days but facilitating diapause induction at short days. This phenomenon could be related to the fact that fluctuating temperature is known to be more optimal for ant development than constant regimes (Lopatina and Kipyatkov, 1990a,b) and thus thermoperiods could be more optimal also for photoperiodic responses reinforcing their effects. On the other hand it is difficult to explain why the same effect does not exist in *M. ruginodis*.

Table 5. *Duration of seasonal cycle and number of rapid brood produced in cultures of Myrmica ruginodis from Belgorod population under thermoperiods or constant temperature at long or short days (after artificial hibernation).*

<table>
<thead>
<tr>
<th>Experimental regimes and parameters</th>
<th>Periods (in days) of:</th>
<th>Rapid brood pupae number</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>eggs presence</td>
<td>rapid brood pupation</td>
</tr>
<tr>
<td>17.5°C min 20 h max n = 5 mean  S.D.</td>
<td>93  115  10.1  a 103 10.1</td>
<td>2  32  11.5  b 20 12.5</td>
</tr>
<tr>
<td>10/25°C min 20 h max n = 5 mean  S.D.</td>
<td>146  229  34.2  a 183 34.2</td>
<td>23  71  20.2  b 50 13.2</td>
</tr>
<tr>
<td>17.5°C min 12 h max n = 5 mean  S.D.</td>
<td>97  129  13.9  a 104 13.9</td>
<td>14  34  7.3  b 22 3.3</td>
</tr>
<tr>
<td>10/25°C min 12 h max n = 6 mean  S.D.</td>
<td>121  139  6.4  a 129 6.4</td>
<td>11  54  14.1  b 35 16.4</td>
</tr>
</tbody>
</table>

The identical letters in the same column denote the means that differ significantly (P<0.95) from each other (the comparison was done only between thermoperiods and constant temperatures under long and short day regimes separately).

Another explanation is that the effects observed might be related not to species differences but instead to geographic variation in each species, i.e. the effect of thermoperiods facilitating the diapause induction at short days might be not a specific property of *M. rubra* but a characteristic of all St. Petersburg *Myrmica* populations. Our experiment can not resolvetthis possibility because at short-day conditions we studied *M. ruginodis* only from Belgorod population and *M. rubra* only from St. Petersburg region. These results should be, therefore, considered as preliminary. More experimental studies on *Myrmica* species from different regions are needed to understand clearly the role of thermoperiods in the seasonal cycle control and the nature of geographic variation of photoperiodic and thermoperiodic responses in ants.

Acknowledgements

This study was sponsored by European Union INTAS programme (grant No 94-2072) as well as by Russian Foundation of Basic Research (grant No 97-04-48987). We thank both these organisations for their support for our research. We are also very much obliged to Dr. G. W. Elmes for his valuable help in revising the manuscript and correcting our English.
References


